

Information Is Where You Find It

DAVID B. DUSENBERY

School of Biology, Georgia Institute of Technology, Atlanta, Georgia 30332-0230

Abstract. A basic problem of foraging is how to obtain information about the location and quality of food. Relevant information is obtained from immediate stimulation, from previous sensory experience stored in memory, and through the genes. Apparently, even the simplest organisms can use information from all these sources. A good example comes from infective juveniles of the plant-parasitic nematode *Meloidogyne incognita*, which only feed after they locate the root of a suitable host plant. Available evidence indicates that carbon dioxide from host roots attracts the juveniles but that it would also be useful for the juveniles to move to an optimal soil depth in which to search for chemical gradients. Although there are few cues to soil depth, *M. incognita* is able to solve this problem in a surprising way. Juveniles can orient to extremely shallow temperature gradients that are nearly always present in the environment. The juveniles also have the peculiar property of moving toward a preferred temperature that is set several degrees above the temperature to which they are acclimated. Computer modeling of this behavior demonstrates that it provides a mechanism for moving to a particular soil depth. Although average temperature is the same at all depths, the amplitude of daily temperature variation declines with depth and provides the required information, which is extracted by interactions among environmental temperature, preferred temperature, rate of acclimation, rate of locomotion, and temperature range of locomotion. Pseudoplasmodia of the slime mold *Dictyostelium* have similar capabilities. This behavior resembles true navigation in that the stimulus used for guidance has no connection to the goal and suggests that even simple or-

ganisms can extract useful information from surprisingly complex stimulus patterns.

Introduction

In foraging for food, a basic problem that animals face is how to make good decisions about finding food and accessing its quality. Plants and microorganisms face analogous problems. Plants compete for sunlight and make choices about how tall to grow based on information about competing plants nearby (Bradburne *et al.*, 1989; Ballaré *et al.*, 1990). Heterotrophic bacteria and protozoa frequently swim up gradients of nutrients to obtain higher concentrations (Armitage and Lackie, 1990). Fungal hyphae grow up similar gradients (Griffin, 1994, pp. 150–151). Photosynthetic microbes swim toward optimal light intensities (Nultsch and Häder, 1988). I will argue that probably all organisms extract and use information in their environment, sometimes in surprising ways.

These behavioral decisions are invariably based on several kinds of information about the environment. By information, I mean simply an agent (energy or chemical) that is important *only* because it is often associated with states of the environment that have inherent importance to the organism (Fig. 1). In other words, all the kinds of agents that act on an organism can be grouped into causal agents that are inherently important because of the chemical or physical effects that they exert and informational agents that are important only because of their association with some causal agent. For example, a chemical carries information if it affects the organism without providing nutritional needs or having toxic effects. A fundamental property of information is that it can easily be ignored by an organism, and special mechanisms are required to capture and store information. As a corollary, information is usually carried by lower

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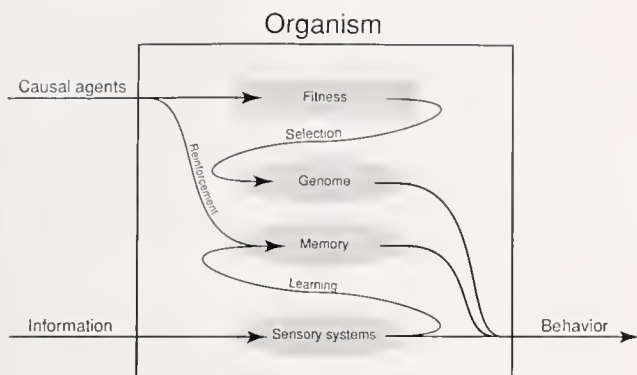


Figure 1. Diagram of relationships between an organism and its environment. On the left are the two types of influences on an organism, and on the right its impact on the environment is represented by its behavior. Shaded ovals indicate the types of information within the organism.

concentrations of chemicals or weaker physical forces than those that directly affect an organism. The scent and color of a flower have importance to a bee only because they are associated with nectar (or pollen), which has nutritional value to the bee. Thus, the scent and color carry information about the presence of nectar or pollen.

As indicated in Figure 1, behavioral activities are regulated by information from three distinct sources: genome, memory, and sensations. The process of selective reproduction results in a store of information in the genome about what decisions and behaviors have been successful in the past for an organism's ancestors. The process of learning results in a store of information in memory about what behaviors have been productive for the individual organism previously. The senses provide information about the current state of the environment. Each of these sources of information thus works over a different time scale and is complementary to the others. I propose that all organisms probably make use of all three types of information, when learning and memory are defined functionally, which leads to the inclusion of sensory adaptation, acclimatization, and habituation (Dusenbery, in press).

One of the most fascinating questions in biology is this: what do organisms know about their environment? In other words, what information do they obtain? This question is difficult to answer for animals other than ourselves and becomes increasingly difficult as organisms differ more from us. A revelation of this century is that some animals can extract information that humans cannot. The ultraviolet light capabilities of insects and the echolocation abilities of bats and whales are clear examples. But what about plants and microorganisms? As we look at simpler organisms, we expect to find more lim-

ited use of information. But how limited? And what information do they obtain? These questions have not been studied very extensively.

In this paper, I present an example of surprising abilities to extract useful information from the complex pattern of temperature changes found in soil in temperate environments by such seemingly simple organisms as nematodes and slime molds.

Patterns of Temperature Change in Soil

Sunlight falling on land surfaces causes relatively large changes in temperature. Daily changes of tens of degrees in the air and soil close to the surface are common as the soil is heated during the day and radiates heat away to the sky at night. Heat travels through soil primarily by conduction and, in most cases, the flow of heat and resulting temperature can be accurately estimated by assuming conduction of heat through a uniform solid (Campbell, 1977). For simplicity, one assumes that the heating and cooling at the surface follows a sinusoidal pattern. Even though the surface temperature pattern is not really sinusoidal, at increasing depths higher frequency components damp out faster than lower frequency components, and a sinusoidal variation with the appropriate fundamental period is a good approximation.

With these assumptions, the temperature at a depth z and time t is described by the equation (Dusenbery, 1992a, p. 115)

$$T(z,t) = T_{ave} + T_{1/2} \exp\left(-\frac{z}{z_d}\right) \sin\left(2\pi \frac{t}{p} - \frac{z}{z_d}\right)$$

where

- T_{ave} is the average temperature at all depths,
- $T_{1/2}$ is half the amplitude of the temperature variation at the surface,
- p is the period of the variation,
- z_d is called the damping depth and equals the square root of the period times the thermal diffusivity of the soil divided by pi ($\sqrt{pD/\pi}$).

For daily variations in temperate zones of the earth, typical values are $z_d = 10$ cm, and $T_{1/2} = 15^\circ\text{C}$. The wavelength of the temperature wave is about 70 cm, and the speed of penetration about 3 cm/h. For annual variations, $z_d = 200$ cm. Within 30 cm of the surface, the temperature gradients are determined primarily by daily variations. From 40 cm to a few meters, annual variations dominate. And temperatures at depths of hundreds to thousands of meters reflect changes in climate.

This temperature pattern establishes vertically oriented temperature gradients, which can guide organisms

upward or downward. At any given depth, warmer temperatures are upward half the day and downward otherwise, but the timing of the change is delayed and the amplitude of the gradients declines with increasing depth. How large are the gradients? The flow of heat from the earth's interior generates an average temperature gradient of $6 \times 10^{-4} \text{ }^\circ\text{C/cm}$. Much larger gradients are usually present near the surface, with 1°C/cm being common in the top few centimeters (Dusenbery, 1988a).

Root-Knot Nematodes, an Example

Nematodes are among the simplest animals with a centralized nervous system. Those that have been studied have a total of only 200 to 300 neurons (Stretton *et al.*, 1978; Chalfie and White, 1988). The root-knot nematodes (*Meloidogyne*) are parasites of plant roots. The spherical adult female develops at a site in a plant root that she never leaves, and she releases eggs to the exterior of the root (de Guiran and Ritter, 1979). The eggs hatch into vermiform second-stage juveniles. These microscopic worms do not feed and must locate an appropriate root before their energy reserves are depleted (in a few weeks during summer). Consequently, the infective juveniles are good models for studying behavioral mechanisms because it is clear that their goal is to move to an appropriate root.

Our experimental studies utilized the southern root-knot nematode (*Meloidogyne incognita*) collected from tomato plants (Diez and Dusenbery, 1989b). Uninfected tomato plants were used as a source of chemical stimuli. Several aspects of nematode behavior were studied by computer tracking methods that recorded the average rate of locomotion of about 200 individuals every few seconds (Dusenbery, 1992b). More traditional methods of observing their net migration on agar surfaces after a period of hours were also used (Diez and Dusenbery, 1989b).

In an extensive search for chemicals emanating from host plants that *M. incognita* infective juveniles might use to locate appropriate roots, we found attraction to carbon dioxide (Pline and Dusenbery, 1987; McCallum and Dusenbery, 1992) but not to any other chemical, although there were also some repellent chemicals released by tomato plants (Diez and Dusenbery, 1989b).

Many root-parasitic nematodes have been found to respond to very shallow temperature gradients (El-Sherif and Mai, 1969), and *M. incognita* does as well, but more detailed experiments revealed that the response was complex. *M. incognita* juveniles moved toward a preferred temperature from both higher and lower temperatures (Diez and Dusenbery, 1989a). This preferred temperature was shifted during acclimation to a different

ambient temperature but was always several degrees above the acclimating temperature. In an appropriate temperature range, they responded to gradients as shallow as 0.001°C/cm (Pline *et al.*, 1988) and showed behavioral responses to temperature changes estimated to be less than 0.001°C (Dusenbery, 1988c). Thus, in the natural environment, they are nearly always in a temperature gradient large enough to influence their locomotion.

What could be the function of such a sensitive but complex response? Due to the dynamic pattern of temperature change in soil near the surface, it was difficult to predict how the nematodes would move, and I turned to computer modeling to address the question (Dusenbery, 1989).

Initial models indicated that estimates of the rate of thermal acclimation and of the width of the temperature range over which the nematodes were active were also needed. More precise data on these parameters were available for the nematode *Caenorhabditis elegans* (Dusenbery *et al.*, 1978; Dusenbery and Barr, 1980), and these values were used as the best available estimates of what *M. incognita* would do. Thermal acclimation occurred with a half time of 2 h, and the temperature range of activity was about 12°C .

As shown in Figure 2, the computer model predicted that during a daily temperature cycle the nematodes would move upward during one or two intervals during the day and downward at other times (Dusenbery, 1989).

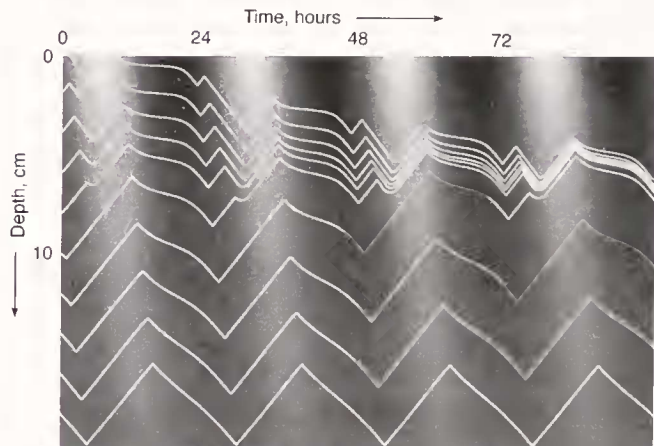


Figure 2. Computed tracks of an organism with the properties estimated for the southern root-knot nematode, *Meloidogyne incognita*. The gray shading represents temperature, with the lighter shades corresponding to higher temperatures. The soil surface is at the top and a depth of 42 cm at the bottom. Time increases to the right over a period of 4.2 days. The white lines record positions of the organisms through time. The various tracks are for organisms starting at depths differing by 5 cm.

However, the distances moved usually did not balance, and the nematodes gradually drifted upward or downward. Most interestingly, nematodes starting out within the top 15 cm of soil all drifted toward a depth of about 5 cm and continued indefinitely to move within a small range at this depth. This "preferred" depth may coincide with a presumed optimal depth at which to search for chemical gradients leading to an appropriate plant root. These modeling results suggest that the thermotactic behavior of these nematodes serves the function of guiding them to an appropriate soil depth and demonstrates that this behavior can extract useful depth information from the complex and dynamic pattern of temperature change.

Nematodes starting out deeper than 15 cm gradually drifted downward until the temperature gradient due to daily fluctuations decays below gradients due to other causes. For example, the average gradient magnitudes of the daily and annual periods are equal at a depth of 30–40 cm (Dusenbery, 1988a; Dusenbery, 1992a, p. 116). It is supposed that relatively few nematodes hatch at these greater depths and that this constant downward movement is a nonfunctional side effect of the mechanism that guides most nematodes toward the optimal depth for finding roots.

Tests of the sensitivity of this behavior to changes in values of the model's parameters demonstrated that the same general pattern of behavior occurs for a wide variety of values (Dusenbery, 1989). However, the rate of locomotion had to be less than 1 cm/h, the temperature range of activity less than 16°C, and the offset of the preferred temperature from the acclimation temperature within the range of 3–5°C.

Although measurement of nematode movement in soil is difficult, Forest Robinson has obtained experimental evidence supporting the hypothesis that *M. incognita* does migrate under the guidance of natural patterns of temperature fluctuation (Robinson, 1994).

Slime Molds, an Example

The other organism that has been demonstrated to have comparable thermal sensitivity is the slime mold *Dictyostelium discoideum* (Bonner *et al.*, 1950; Poff and Skokut, 1977; Whitaker and Poff, 1980). Unlike juveniles of *M. incognita*, pseudoplasmodia of *D. discoideum* move away from a temperature about 2°C below its acclimation temperature. As shown in Figure 3, computer modeling of this behavior, using the best available estimates of the appropriate values of the parameters, demonstrates that pseudoplasmodia starting out within 20 cm of the surface move toward the surface (Dusenbery, 1988b). This movement is even more clearly func-

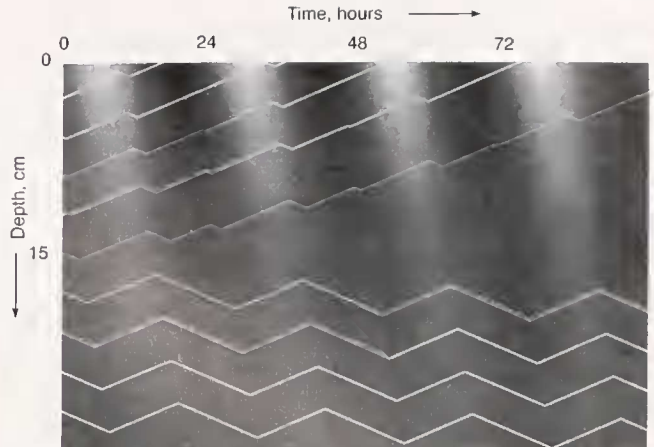


Figure 3. Computed tracks of an organism with the properties estimated for the pseudoplasmodia of the slime mold, *Dictyostelium discoideum*. The parameters are 0.2 cm/h rate of locomotion, 0.2 /h rate of temperature adaptation, -2°C offset of the avoided temperature from the adapted temperature, and an unlimited temperature range of locomotion. Other features as in Figure 2.

tional than the nematode movement. After a period of migration, the pseudoplasmodia form a fruiting body and release spores from the top of a stalk. The spores will be dispersed much more effectively if released at the surface of the soil where wind can carry them. Thus, it appears that even the "simple" slime mold has developed a mechanism for extracting information about depth from complex patterns of temperature change.

Conclusion

In both examples we see a surprising ability of a simple organism to extract and use information from a complex stimulus pattern. In both cases, the behavior is analogous to navigation, because the stimulus used to guide locomotion is not connected to the goal. Such subtle mechanisms may have evolved because alternative stimuli with a simpler relationship to soil depth are lacking. Similar mechanisms could be used by any organism that needs to move with respect to a surface that is subjected to regular heating and cooling (for example, organisms living in a tree trunk). These findings should cause us to look for other situations in which organisms find information where we would not expect it.

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